

REPRODUCTIVE ANATOMY AND MORPHOLOGY OF MYRTALES IN RELATION TO SYSTEMATICS¹

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Evidence from reproductive morphology and anatomy (excluding palynology) favors an inclusive Myrtales of 11 core families (see below) over either a much broader Myrtales, as advocated, for example, by the Englerian school (most recently Melchior, 1964) or a narrower Myrtales and accompanying Lythrales, as advocated by Novák (1961, 1972) and more recently and in a rather different manner by Briggs and Johnson (1979), who, however, withdrew their concept in this symposium (Johnson & Briggs, 1984; see also argumentation in the appendix in Schmid, 1980). Embryology provides the best evidence for a concept of core Myrtales consisting of Combretaceae, Crypteroniaceae, Lythraceae, Melastomataceae sensu lato, Myrtaceae (including Psiloxylaceae³ and Heteropyxidaceae; Schmid, 1980), Oliniaceae, Onagraceae, Penaeaceae, Punicaceae, Sonneratiaceae, and Trapaceae (familial arrangement strictly alphabetical; see also Tobe & Raven, 1983a).

The following embryological traits unite core Myrtales: anthers tetrasporangiate*, with conspicuous endothecium*, glandular tapetum, simultaneous cytokinesis; ovules anatropous*, bitegmic*, crassinucellate; antipodals ephemeral or absent*; endosperm nuclear*; seeds exalbuminous*. The asterisks indicate that exceptions are known. Table 1 (pp. 834–835) lists such exceptions, which in some cases are known for only one family or even only one species, for example, the trisporangiate anther of *Corynanthera flava* of Myrtaceae (Green, 1979). Other embryological features such as nuclear condition of pollen at time of shedding, persistence of anther epidermis, and types of anther wall development, embryo sac, and embryogeny vary appreciably (see Table 1). Significantly, Dahlgren and Thorne

(1984) and Tobe and Raven (1983a) independently arrived at a very similar complex of embryological characters unifying core Myrtales.

Reproductive anatomy, that is, histology and vasculature, gives no special aid in resolving the makeup of Myrtales. Features such as bicollateral bundles (internal or intraxylary phloem) occur in peduncles, inflorescence axes, pedicels, flowers, and fruits of most myrtalean taxa (Schmid, 1972b, 1980, for Myrtaceae and Lythraceae; Schmid, unpubl. data and literature survey for other families). However, bicollateral bundles are really histological markers first described for vegetative parts of Myrtales and other orders (Cronquist, 1981; Dahlgren & Thorn, 1984; Metcalfe & Chalk, 1983; van Vliet & Baas, 1984) and then applied to their reproductive parts. The same pertains to vestured pits, which are unreported for myrtalean reproductive structures, but which occur in Lythraceae, Melastomataceae, Myrtaceae, *Alzatea* (Schmid, unpubl. data). In Myrtales, amphicribal bundles are common, especially in androecia and placentae (Schmid, 1972b, 1980, for Myrtaceae and Lythraceae; Schmid, unpubl. data and literature survey for other families). However, amphicribal bundles seem related to functional, nutritional factors for reasons elaborated elsewhere (Schmid, 1976, 1978).

There are no unifying features of floral vasculature for Myrtales (nor for other orders), let alone Myrtaceae. An axile ovular supply (Schmid, 1972a) is most common and clearly basic; the derived transeptal ovular supply (Schmid, 1972a) occurs variously in Myrtaceae, Oliniaceae, Onagraceae, Punicaceae, and *Rhynchocalyx* of core Myrtales (Eyde, 1981; Schmid, 1972a, 1972b, 1980, unpubl. data and literature survey), as well as in Lecythidaceae sensu lato, Rhizophoraceae

¹ Text expanded somewhat from my symposium abstract (Schmid, 1981), with added references and table. A detailed account will be published in a future issue of this journal. In the interim Dahlgren and Thorne (1984) should be consulted, especially for discussion of embryological features. A detailed review of embryology of Myrtales has also been published by Tobe and Raven (1983a—see also comment in note a to Table 1). Supported in part by NSF grants BMS75-03811 and DEB78-04289.

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³ Pollen morphology, sunken styles, and the occurrence of secretory cavities in all aerial organs are the strongest arguments for including *Psiloxylon* in Myrtaceae, albeit as a separate subfamily, Psiloxylloideae (see Schmid, 1980).

sensu lato, and Thymelaeaceae, which were previously attributed to Myrtales (see Dahlgren & Thorne, 1984).

Various families can be fairly safely excluded from the aforecircumscribed core Myrtales on the basis of a combination of characters from both embryology and vegetative anatomy. For example, Rhizophoraceae sensu lato, Lecythidaceae sensu lato, Theligonaceae, Cynomoriaceae, Hippuridaceae, among others, lack bicollateral bundles and vested pits and in some cases (Rhizophoraceae, Lecythidaceae) also have scalariform perforation plates (Cronquist, 1981; Dahlgren & Thorne, 1984; Metcalfe & Chalk, 1983; van Vliet & Baas, 1984), all of which are non-myrtalean attributes. And especially tenuinucellate and/or unitegmic ovules, which occur variously in Lecythidaceae sensu lato, Hippuridaceae, and Theligonaceae are significant in excluding these families from core Myrtales. Thymelaeaceae, however, have vested pits and bicollateral bundles (Cronquist, 1981; Dahlgren & Thorne, 1984; Metcalfe & Chalk, 1983; van Vliet & Baas, 1984) and on the basis of wood anatomy (van Vliet & Baas, 1984), embryology (Table 1), and other aspects of reproductive anatomy and morphology (Cronquist, 1981; Dahlgren & Thorne, 1984; Schmid, unpubl. data) cannot be easily excluded from core Myrtales. Pollen and chemical evidence, nevertheless, do favor such an exclusion (Dahlgren & Thorne, 1984). There are, of course, additional arguments relevant to the aforementioned and other familial exclusions (see Dahlgren & Thorne, 1984; Orchard, 1975; Tobe & Raven, 1983a).

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TABLE 1. Some embryological features of core Myrtales and Thymelaeaceae.^a

	Combreta	Cryp- tero	Lythrace	Melastom ^b	Myrtacea ^b
Number genera/species	20/400	3/10	29/590	200/4,000+	149/3,675
Number sporangia/anther	4	4	4	4	4(3) ^c
Anther with conspicuous endothecium at maturity	yes	no	yes	no (yes) ^d	yes
Anther with glandular tape- tum	yes	yes	yes	yes	yes
Anther with simultaneous cytokinesis	yes	yes	yes	yes	yes ^e
Ovules anatropous	yes	yes	yes, very rare other ^f	yes, very occ. other ^f	yes, occ. other ^f
Ovules bitegmic	yes	yes	yes	yes	yes, very occ. uni ^g
Ovules crassinucellate	yes	yes	yes ^h	yes	yes
Antipodals	ephemeral, persistent ⁱ	ephe- meral	ephemeral	ephemeral	ephemeral
Endosperm (initial)	nuclear	nu- clear	nuclear	nuclear	nuclear
Seeds exalbuminous	yes	yes	yes	yes	yes, occ. no ^j
Anther epidermis persistent	yes	yes	no	yes	occ.
Type of anther wall devel- opment	Basic ^l	Dicot	Dicot	irregular ^m	Basic ⁿ
Pollen at shedding	bi-, occ. trinuc	binuc	binuc	trinuc	binuc
Type of embryo sac	Polygonum, Panaea ^p	Poly- gon- um	Polygonum	Polygonum	Polygonum
Type of embryogeny	Asterad	??	Onagrad	Onagrad (So- lanad) ^q	Onagrad (irreg) ^r

^a Embryological features considered as unifying the 11 families of core Myrtales (arrangement of families strictly alphabetical; see also note b) are above the line; more variable embryological features are below the line. On embryology alone Thymelaeaceae could be included in Myrtales, but other evidence excludes this family (Dahlgren & Thorne, 1984). Some conspicuous exceptions are elaborated below. Descriptors such as "rarely," "occasionally," etc. are used as defined in Schmid (1982). Number of genera/species per family from Dahlgren and Thorne (1984) and Schmid (1980). Source of other data: Corner (1976), Cronquist (1981), Dahlgren and Thorne (1984), Davis (1966), Orchard (1975), Schmid (1972b, 1980), Tobe and Raven (1983b); references therein and below, other recent taxonomic and anatomical literature, and unpubl. data on various families.

This table was compiled independently of Tobe and Raven (1983a), which appeared while the present article was in press. These authors noted (pp. 87-88): "Thymelaeaceae differ from [core] Myrtales in possessing (1) a thick, 3- to 4-layered inner integument; (2) micropyle formed by the inner integument alone; (3) persistent antipodal cells that often multiply; and (4) albuminous seeds. Embryologically, these differences are decisive in ruling out any direct relationship between Thymelaeaceae and core Myrtales." Feature (1) is apparently unique to the family, but its overall systematic significance in angiosperms is unclear. Features (2) and (3) occur in core Myrtales, but are exceptional there (see Tobe & Raven and note i below). The old literature Tobe and Raven cite for feature (4) is not in agreement with the newer conclusion of Corner (1976) given in note k. Tobe and Raven did not cite Corner and also were unaware of the exception indicated in note j. I thus am less impressed than Tobe and Raven by the embryological distinctiveness of Thymelaeaceae from core Myrtales, in part because various families of the latter have peculiar embryological features. In other respects, Tobe and Raven and I are in substantial agreement regarding the embryological features unifying core Myrtales.

Key: binuc = binucleate; occ. = occasionally; trinuc = trinucleate; ? = information should be verified by critical examination; ?? = situation not known on basis of literature consulted and/or material examined.

^b Melastomataceae including Memecylaceae fide Dahlgren and Thorne (1984). Myrtaceae including Psiloxylaceae and Heteropyxidaceae fide Schmid (1980, see text note 2). Embryological features of Psiloxylaceae and Heteropyxidaceae as far as is known correspond precisely with those of core Myrtaceae (Schmid, 1980).

^c Trisporangiate only in *Corynanthera flava* (Green, 1979).

^d Endothecium poorly developed and lacking fibrous thickenings in Melastomatoideae, but conspicuous, even with fibrous thickenings, in Memecyloideae (see Davis, 1966).

TABLE 1. Continued.

Oliniace	Onagrace	Penaeace	Punicace	Sonnerat	Trapacea	Thymelae
1/10	17/670	5/25	1/2	2/7	1/3	50/500
4	4	4	4	4	4	4
yes	yes	??	yes	yes	yes	yes
?yes	yes	??	?yes	yes	yes	yes
??	yes	??	??	yes	yes	yes
no ^f	yes	yes	yes	yes	yes	yes, to other ^f
yes	yes	yes	yes	yes	yes	yes
yes ephemeral	yes absent	yes ??	yes ephemeral	yes ephemeral	yes ephemeral or absent	yes persistent ⁱ
nuclear	nuclear	nuclear	nuclear	nuclear	ephemeral (nuclear) or absent	nuclear
yes	yes	yes	yes	yes	yes	yes, occ. no ^k
??	yes	??	?yes	yes	yes	yes
?Dicot	??	??	??	Dicot	Dicot	Basic, Mono- cot ^o
??	binuc	??	binuc	binuc	binuc	trinuc
Polygonum	Oenothera	Penaea	Polygonum	Polygonum	Polygonum	Polygonum
??	Onagrad	Asterad	??	Onagrad	Solanad	Asterad

^e No information in Davis (1966), but more recently simultaneous cytokinesis reported (Davis, 1968, 1969; Prakash 1969b, 1969c, 1969d, 1969e—citations in Schmid, 1972b).

^f Ovules of Oliniaceae hemitropous to campylotropous (Dahlgren & Thorne, 1984). Ovules of Lythraceae also very rarely amphitropous (Schmid, 1980), of Melastomataceae also very occasionally campylotropous (Cronquist, 1981; other taxonomic literature), of Myrtaceae also occasionally campylotropous or other—hemitropous, amphitropous (Schmid, 1980), of Thymelaeaceae anatropous to hemitropous (Cronquist, 1981; Davis, 1966).

^g Unitegmatic ovules reported for five species of *Syzygium* sensu Schmid (1972a, 1972b), including some species formerly included under *Eugenia* (Davis, 1966).

^h Nucellus of *Ammannia coccinea* is two-layered and regarded as tenuinucellate by Smith and Herr (1971). However, by conventional definitions this is crassinucellate or, at best, subcrassinucellate.

ⁱ *Guiera senegalensis* (monotypic) of Combretaceae has persistent, multiplicative antipodals (Davis, 1966; Venkateswarlu & Prakasa Rao, 1972), the only known member of core Myrtales with this feature, and thus similar to Thymelaeaceae with persistent, usually multiplicative antipodals.

^j Endosperm occasionally scantily present according to Corner (1976), Petit (1908—citation in Schmid, 1980), Schmid (1980), and taxonomic literature.

^k Endosperm “commonly absent from the seed or reduced to a trace, but copious in *Lachnaea* and *Pimelea*” (Corner, 1976: 270; see also Cronquist, 1981). See also note a.

^l Anther development irregular, with only one middle layer, in *Guiera senegalensis* (Davis, 1966; Venkateswarlu & Prakasa Rao, 1972).

^m Anther development irregular and not characterized according to type by Davis (1966) or other workers.

ⁿ No information in Davis (1966), but more recently anther development reported to be of Basic type (Davis, 1968, 1969; Prakash, 1969b, 1969c, 1969d, 1969e—citations in Schmid, 1972b).

^o Basic type in *Wikstroemia canescens*, Monocotyledonous type in *Lasiosiphon eriocephalus* (Davis, 1966).

^p The report of the tetrasporic *Penaea* type embryo sac for two species of *Combretum* needs confirmation (see Dahlgren & Thorne, 1984; Tobe & Raven 1983a; Venkateswarlu & Prakasa Rao, 1972).

^q Solanad embryogeny type in *Melastoma malabathricum* and *Sonerila wallichii* (Davis, 1966).

^r Irregular embryogeny in *Darwinia fascicularis*, *D. micropetala*, and *Angophora floribunda* (Prakash, 1969d, 1969e—citations in Schmid, 1972b).